



# Effects of free-ranging cattle and landscape complexity on bat foraging: Implications for bat conservation and livestock management



L. Ancillotto<sup>a,1</sup>, A. Ariano<sup>a</sup>, V. Nardone<sup>a</sup>, I. Budinski<sup>b</sup>, J. Rydell<sup>c</sup>, D. Russo<sup>a,d,1,\*</sup>

<sup>a</sup> Wildlife Research Unit, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, Portici (Na), Italy

<sup>b</sup> Department of Genetic Research, Institute for Biological Research "Siniša Stanković", University of Belgrade, Serbia

<sup>c</sup> Biology Department, Lund University, Lund, Sweden

<sup>d</sup> School of Biological Sciences, University of Bristol, UK

## ARTICLE INFO

### Article history:

Received 13 January 2017

Received in revised form 27 February 2017

Accepted 1 March 2017

Available online xxx

### Keywords:

Insectivory

Farming

Parasites

Pest suppression

Traditional pastoralism

## ABSTRACT

Traditional agropastoralism increases biodiversity by maintaining habitats whose existence depends on human practices as well as by providing wildlife, including bats, with key spatial and trophic resources. Bats in farmland are crucial predators of crop pests, thus offering an economically important ecosystem service. It seems possible that bats may also provide services by feeding on insects associated with livestock. We tested whether bats forage over cattle in a traditionally managed pastoral area of central Italy, i.e. setting the bases for providing pest control services. We found that small bat species (mostly *Pipistrellus* spp.) foraged preferentially over livestock, and that their activity increased, but then reached a plateau or slightly decreased, for progressively larger herds. Landscape complexity also led to an increase in bat activity over livestock. Since insects attracted to cattle at night typically include flies such as mosquitoes (Culicidae) and biting midges (Ceratopogonidae), which are potentially harmful to cattle and may carry serious diseases, and that bats such as *Pipistrellus* spp. are important predators of such flies, we argue that bats may play a valuable pest-suppression role.

© 2017 Elsevier B.V. All rights reserved.

## 1. Introduction

One of the main consequences of human impact over half of the Earth's land surface (Hooke et al., 2012) is the existence of a complex network of interactions with wildlife, some conspicuous, others subtle, whose comprehensive understanding plays a pivotal role in tailoring effective conservation practices (Caro et al., 2012). Loss of habitat due to replacement of natural land cover with urban and agricultural areas is one of the main drivers of the current biodiversity loss worldwide (Singh, 2002; Turner et al., 2007). While most species succumb, a limited number of adaptable species tolerate or even benefit from large-scale habitat disappearance or alteration (Parker and Nilon, 2012), at the expense of community diversity and the ecosystem services it provides (e.g. Morelli et al., 2016).

Agriculture is one of the most powerful drivers of land use change. An estimated 13% and 26% of the planet's land surface have

been converted to cropland and permanent meadows and pastures, respectively (Hooke et al., 2012). Livestock farming is the most widespread human activity, dominating rangeland ecosystems worldwide (Fleischner, 1994; Alkemade et al., 2013). The negative ecological effects of free-range livestock farming comprise biomass removal, vegetation trampling, root destruction, competition with wild ungulates (e.g. Alkemade et al., 2013) and transmission of diseases to wildlife (Smith et al., 2009). However, the type and magnitude of these effects vary according to the extent of habitat grazed, the type of land management applied and whether grazed areas result from conversion of former forest (Alkemade et al., 2013). While intensive farming is responsible for a large-scale decline of biodiversity, low-intensity farming systems, including traditional agricultural and pastoral practices, have rather played a chief role in creating a diverse range of landscapes that sustain rich biological communities including many wildlife species at risk throughout Europe (Moreira et al., 2005). For example, some eastern Mediterranean pastures have actually survived thanks to uninterrupted livestock grazing for over 5000 years (Blondel and Aronson, 1999). Land abandonment – i.e. the cessation of agriculture and pastoralism in previously farmed landscapes driven by major socio-economical changes – is recognised as a major driver of the disappearance of important

\* Corresponding author at: Wildlife Research Unit, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, via Università 100, 80055, Portici (Na), Italy.

E-mail address: [danrusso@unina.it](mailto:danrusso@unina.it) (D. Russo).

<sup>1</sup> These authors contributed equally to this work.

habitats and species whose existence depends on human action (Moreira and Russo, 2007).

Grazing by free-ranging domestic stock has taken over the ecological role of the extinct large herbivores such as aurochs (*Bos primigenius*) and wild horses (*Equus ferus*) that dominated Europe in late Pleistocene and early Holocene in creating and maintaining open landscapes of great value for biodiversity (Hearn, 2015). Besides having direct effects on habitat structure, livestock also represent a direct food source for vertebrates such as large predators (Boitani, 2000) and scavengers (Donazar et al., 2002). Moreover, many coprophagous insects feed on dung (Lumaret and Kirk, 1987), providing prey to insectivorous vertebrates such as birds (Wilson et al., 1999) and bats (Duvergé and Jones, 2003). In some cases, the mere presence or activity of livestock may favour prey availability to insectivores. A familiar example is the cattle egret (*Bubulcus ibis*), often feeding among cattle on insects set in motion by grazing (Heatwole, 1965; Wahungu et al., 2003), so that the presence of livestock has helped this bird to increase its geographical range (Petretti, 2003).

Bats are a biodiverse mammal order providing crucial ecosystem services in both natural and agricultural ecosystems including seed dispersal or pest suppression (Kunz et al., 2011). Given the high sensitivity of bats to human interferences (Jones et al., 2009; Russo and Jones, 2015) many bat populations have shown marked declines in response to land use change and, as for many other taxa, agricultural intensification constitutes a powerful driver of habitat reduction and fragmentation (Heim et al. 2016; Park, 2015). Low-intensity agriculture such as organic farming (Wickramasinghe et al., 2003) or traditionally managed cultivations (Russo et al., 2002, 2005), instead, host higher levels of bat abundance, diversity and foraging activity (Park, 2015). Although the mechanisms generating such patterns are unclear (Park, 2015), several potentially important causal factors may be identified, e.g.: the persistence of high spatio-temporal habitat heterogeneity (Benton et al., 2003); the partial or complete avoidance of pesticides that are widespread in intensive agriculture, where they affect bats through both biomagnification (Jefferies, 1972) and prey depletion (Wickramasinghe et al., 2004); and the presence of small-scale habitats such as hedgerows (Downs and Racey, 2006; Boughey et al., 2011) and water bodies (Korine et al., 2015).

In contrast to intensive farming practices (Park, 2015), moderate livestock grazing may favour bats by maintaining semi-open habitats favoured by many species (Duvergé and Jones, 2003; López-González et al., 2015), increasing availability of prey (Shiel et al., 1991; Catto et al., 1996; Ransome, 1996) such as dung-dwelling insects (Duvergé and Jones, 2003), and providing artificial drinking sites (Korine et al., 2015; Russo et al., 2016). That several species of bats feed extensively on dung-beetles (Scarabaeidae) and other insects in pastures has been known for a long time (Rydell, 1986) but only recently has it become apparent that bats also feed around the cows themselves (Downs and Sanderson, 2010).

The foraging activity of insectivorous bats may increase crop yields through pest suppression, a vital service in agroecosystems (e.g. Federico et al., 2008; Boyles et al., 2011; McCracken et al., 2012; Maine and Boyles, 2015; Heim et al., 2015; Puig-Montserrat et al., 2015). Although quantitative studies on nocturnal or crepuscular insects parasitizing cattle are missing, it is well known that mosquitoes, biting midges or blackflies have a considerable negative effect on livestock productivity (Davies, 1957; Steelman, 1976; Kazek and Jezierski, 2014): in 1981 an estimated 10% of cattle productivity was lost due to ectoparasites in the US, almost 70% of which was caused by dipterans (Byford et al., 1992). Bats might therefore potentially play an important role in suppressing such pests, acting as mutualists of livestock rather than commensals.

The aim of this study was to investigate if insectivorous bats in a Mediterranean landscape routinely feed over free-ranging cattle, rather than over the dung, as suggested by Downs and Sanderson (2010). We then developed this aspect further by investigating the responses of bat activity and species richness to increasing herd sizes (corresponding to more parasitic insects; Schmidtman and Valla, 1982) and landscape heterogeneity (whose growth typically has positive effects on bat assemblages; Heim et al., 2015), predicting a positive relationship in both cases.

## 2. Materials and methods

### 2.1. Study area

Fieldwork took place in a Site of Community Importance in Castel di Guido, central Italy (41.89 N, 12.31 E, altitude ca 75 m a.s.l.). Part of the area is a bird reserve of the Italian League for Bird Protection (“Oasi Lipu Castel di Guido”). The landscape is characterised by a mosaic of Mediterranean scrublands and oak woodlands (mainly made of *Quercus pubescens* and *Q. suber* standings) interspersed with organic agricultural crops (cereals, alfalfa) and pastures. A few isolated buildings and one small village occur in the area. Water habitats are represented by a few seasonal pools, one anti-fire basin and several cattle troughs. At the site, five free-ranging herds of “Maremmana” cattle are kept in 6.0–9.1 km<sup>2</sup> fenced areas covered with both pastures and natural vegetation, while four “Friesian” and “Chevrolet” cattle herds use 0.5–3.1 km<sup>2</sup> fenced areas dominated by pasture. Livestock were not treated with avermectin or other anti-helminthics in the study area, where farm management is strictly organic.

### 2.2. Sampling design

To achieve sufficient temporal coverage of data collection, our study was done in two years (2015 and 2016) from June to September, comprising crucial phases of bat life cycle such as pregnancy, lactation, juvenile emancipation and mating.

The study area was over 1300 ha, allowing us to include sufficient spatial variation in data collection. Within this area, we selected 13 sampling plots as far apart as possible from each other. Plots had a radius of  $530 \pm 235$  m (mean  $\pm$  standard deviation) and inter-plot distance ranged between 280 and 1900 m. For each plot we recorded bat activity at three different points  $\geq 100$  m apart (one night per point), each of which corresponding to one of the following treatments: (1) cows present (in such cases recordings were made  $< 10$  m from livestock); (2) dung present – cows absent (fresh dung was present, but no cows were present within a radius  $\geq 70$  m around the recording point) and (3) control, i.e. pastures with neither cattle nor dung within  $\geq 70$  m. When sampling in the “cows present” condition, we assessed herd size by visually counting the numbers of head present at the sampling site. On each night two sampling points were taken at random, and recordings were made continuously for 4 h since sunset.

We used D1000X real-time bat detectors (Pettersson Elektronik AB, Uppsala, Sweden) kept in the heterodyne mode and manually tuned continuously between 30 and 100 kHz to cover call frequencies of all species present in the area. When a bat was heard, calls were recorded in real time at 380 kHz sampling rate until 5 s had elapsed since the last detected call.

### 2.3. Sound analysis

Recordings were analysed with BatSound 4.12 (Pettersson Elektronik AB) and identification was carried out by applying the quadratic discriminant functions developed by Russo and Jones (2002). Because that approach requires manual selection and

measurement of echolocation calls, all recordings were double-checked by inspecting spectrograms visually (Russo and Voigt, 2016). At least three *Myotis* species (*M. myotis/blythii*, *M. emarginatus*, *M. nattereri*) are known to occur in the area (L. Ancillotto, pers. obs.), but since many calls did not achieve sufficient classification performances (<80%) we pooled them together as 'Myotis sp.' We quantified bat activity by counting respectively the numbers of bat passes, defined following Kalcounis et al. (1999) and expressing general bat activity, and of feeding buzzes (e.g. Griffin et al., 1960; Vaughan et al., 1997; Russo and Jones, 2003). *Tadarida teniotis* forages very high above ground (Marques et al., 2004) so we ruled out that its activity could be influenced by prey availability near livestock, i.e. we excluded this species by both single-species and community analyses; passes of species rarely detected (n passes <30: *P. pygmaeus*, *Nyctalus leisleri*, *Myotis* sp.) were excluded from single-taxon analyses.

#### 2.4. Data analysis

We generated a 1:25000 habitat map of the area through photointerpretation of orthophotos, provided by the regional authorities that manage the nature reserve where the study was set, and subsequently validated the map through field surveys. Habitats were categorised as (1) open grassland including pastures, (2) woodland and scrubland, (3) riparian habitats, and (4) paved or dirt roads and buildings.

We measured the minimum distances between recording points and respectively buildings and permanent water and, within a radius of 100 m around each point, the following landscape metrics: amount of edge habitat (m), amount of natural vegetation (m<sup>2</sup>), number of patches and Shannon's landscape diversity index. Landscape metrics were calculated with FRAG-STATS v. 4.0 (McGarigal et al., 2012). We employed generalized linear mixed models (GLMMs), using as responses the following variables measured per recording point/night: (1) bat species richness, (2) overall bat activity, (3) activity of species for which >30 passes were available.

Treatment (cows and dung, dung only, control), sampling year (2015 or 2016) and recording month (June, July, August, September) were used as fixed factors, landscape metrics as covariates, herd size was nested within treatment, while recording day and sampling plot were entered as random factors. All variables were first checked for normality with Shapiro-Wilk's tests, and when needed log-transformed to meet GLMM assumptions. When a significant effect of treatment was found, we used Tukey's post hoc tests to establish differences among treatments.

When herd size had a significant effect on a response variable, we explored the relationship between the two variables choosing the best model among linear, polynomial and logistic regressions according to model's adjusted R<sup>2</sup> value. Statistical analyses were run with R 2.13.2 (R Development Core Team, 2011) using the package lme4 (Pinheiro et al., 2016). Significance was set at P < 0.05.

### 3. Results

We recorded a total of 156 h of bat activity, comprising 3963 bat passes of 11 species, or species groups, and 549 feeding buzzes (Table 1). The most abundant species were *Pipistrellus kuhlii*, *Hypsugo savii* and *P. pipistrellus*, followed by *Tadarida teniotis*, *Eptesicus serotinus* and *Rhinolophus ferrumequinum*. Numbers of feeding buzzes were positively correlated with numbers of bat passes (total bat activity: Pearson  $r = 0.80$ ,  $p < 0.01$ , *P. kuhlii*:  $r = 0.61$ ,  $p < 0.01$ , *H. savii*:  $r = 0.74$ ,  $p < 0.01$ , *P. pipistrellus*:  $r = 0.54$ ,  $p < 0.05$ ; *E.*

**Table 1**

Numbers of bat passes, feeding buzzes and percentage of sites (n = 39) where bats were recorded in an agro-pastoral area of central Italy.

Species	N passes	N feeding buzzes	% of sites
<i>Pipistrellus kuhlii</i>	2080	255	100.0
<i>Hypsugo savii</i>	1480	249	100.0
<i>Pipistrellus pipistrellus</i>	123	9	66.6
<i>Tadarida teniotis</i>	117	22	75.5
<i>Eptesicus serotinus</i>	99	12	46.2
<i>Rhinolophus ferrumequinum</i>	39	0	23.1
<i>Myotis</i> sp.	19	2	28.2
<i>Pipistrellus pygmaeus</i>	5	0	7.7
<i>Nyctalus leisleri</i>	1	0	2.6
Total	3963	549	NA

*serotinus*:  $r = 0.71$ ,  $p < 0.05$ ), so we used only the latter in the analyses.

In agreement with our hypothesis, the overall bat activity was influenced by the presence of cows, with a strong positive effect of herd size (Table 2). According to pairwise comparisons, bat activity over cattle was higher than over dung only ( $p < 0.01$ ), and higher over dung than at control points ( $p < 0.01$ ). Total bat activity was also greater at points surrounded by more diverse landscape mosaics (expressed by the Shannon diversity index;  $p < 0.05$ ) and more edge habitat ( $p < 0.01$ ). Bat species richness was only influenced by habitat diversity, which had a positive effect on the former ( $p < 0.001$ , Table 2). The number of passes of *P. kuhlii* ( $p < 0.01$ ), *H. savii* ( $p < 0.01$ ), *P. pipistrellus* ( $p < 0.05$ ), *E. serotinus* ( $p < 0.05$ ) and *R. ferrumequinum* ( $p < 0.05$ ) were influenced by treatment (Table 2; Fig. 1). They were more frequent over cows than over dung (pairwise comparisons: all  $p < 0.05$ ) and, in both situations, more frequent than at control points (pairwise comparisons,  $p < 0.01$ ), with the exception of *R. ferrumequinum*, which was more active over controls than over dung (Fig. 1). The activity of all species (all  $p < 0.05$ ) except *R. ferrumequinum* also increased with herd size (Table 2) and, with the sole exception of *P. kuhlii*, for increasing amounts of edge habitat (Table 2). *P. kuhlii* was the only species whose activity significantly increased for decreasing distances from water ( $p < 0.05$ ), while *R. ferrumequinum* was more active ( $p < 0.01$ ) at points surrounded by a more diverse landscape mosaic (Table 2).

In all models, neither sampling year or month influenced species activity, total bat activity or species richness (Table 2).

The relationships between bat activity and herd size were best explained by polynomial regressions: activity first increased steeply and then slowed down, reaching a plateau (total activity, *P. kuhlii*, *H. savii*) or possibly decreasing (*P. pipistrellus*) for progressively larger herd sizes (Fig. 2).

### 4. Discussion

In agreement with Downs and Sanderson (2010) we show that the presence of cattle rather than that of dung is responsible for the high foraging activity bats exhibit over livestock. This difference is most likely explained by the abundance of flies (Diptera) attracted to large herbivores, specifically cattle, including nocturnal or crepuscular blood-sucking forms such as mosquitoes (Culicidae), blackflies (Simuliidae) and biting midges (Ceratopogonidae) (Davies, 1957; Steelman, 1976). In addition, some larger flies such as species of biting house flies (e.g. the stable fly *Stomoxys calcitrans*) and blowflies (*Calliphora* spp.), which normally are diurnal, may also be active at night in warm weather, such as in our case (Stamper and DeBry, 2007). Hence there may be a large array of potentially harmful and blood-sucking flies, some of which acting as vectors of serious pathogens, that occur over cattle at night (Kazek and Jezierski, 2014). The production loss by nocturnal

**Table 2**

Results from generalized linear mixed models testing the effects of cattle (treatment, herd size) and landscape elements on bat activity in an agro-pastoral area of central Italy.

GLMM response	R <sup>2</sup>	Variable	Estimate	Error	Z	P
Species richness	0.42	<i>Intercept</i>	6.82	1.2	5.85	**
		Treatment	−1.71	1.28	3.29	n.s.
		Herd size	1.10	6.68	0.58	n.s.
		Amount of edge habitat	1.45	3.72	0.11	n.s.
		SHDI	0.21	0.02	14.72	***
		N patches	1.15	1.14	0.25	n.s.
		Amount of natural vegetation	4.45	2.80	0.05	n.s.
		Distance from buildings	−4.89	1.97	0.01	n.s.
		Distance from water	−1.78	9.99	3.48	n.s.
		Year	2.12	0.80	2.00	n.s.
		Month	−1.82	0.91	3.02	n.s.
Total bat activity	0.69	<i>Intercept</i>	22.12	3.93	18.10	***
		Treatment	69.78	21.01	12.25	***
		Herd size	4.69	0.75	42.80	***
		Amount of edge habitat	0.02	0.01	8.45	**
		SHDI	21.11	8.57	5.02	*
		N patches	−1.67	3.58	0.68	n.s.
		Amount of natural vegetation	3.19	3.27	0.39	n.s.
		Distance from buildings	0.01	0.06	0.14	n.s.
		Distance from water	−0.03	0.03	0.95	n.s.
		Year	0.11	0.03	1.05	n.s.
		Month	0.07	0.03	0.30	n.s.
<i>Pipistrellus kuhlii</i>	0.68	<i>Intercept</i>	22.52	2.80	8.00	***
		Treatment	47.32	16.21	6.39	**
		Herd size	2.68	0.56	29.61	***
		Amount of edge habitat	0.01	0.01	7.32	*
		SHDI	−7.33	6.79	1.02	n.s.
		N patches	−0.96	2.41	0.21	n.s.
		Amount of natural vegetation	4.16	2.34	2.13	n.s.
		Distance from buildings	−0.01	0.04	0.34	n.s.
		Distance from water	−7.85	4.22	4.09	*
		Year	0.05	0.13	0.49	n.s.
		Month	0.05	0.08	1.08	n.s.
<i>Hypsugo savii</i>	0.51	<i>Intercept</i>	4.36	2.28	11.06	***
		Treatment	4.29	11.5	6.98	**
		Herd size	0.88	0.41	7.89	**
		Amount of edge habitat	0.02	0.01	18.61	***
		SHDI	−0.51	4.64	0.01	n.s.
		N patches	0.02	2.12	0.10	n.s.
		Amount of natural vegetation	−0.60	1.89	0.01	n.s.
		Distance from buildings	−0.04	0.04	0.58	n.s.
		Distance from water	0.03	0.02	0.63	n.s.
		Year	0.01	0.02	<0.01	n.s.
		Month	0.02	0.05	<0.01	n.s.
<i>Pipistrellus pipistrellus</i>	0.34	<i>Intercept</i>	6.78	4.31	1.61	**
		Treatment	1.19	2.50	3.52	*
		Herd size	0.13	0.09	5.30	*
		Amount of edge habitat	0.07	0.01	7.84	n.s.
		SHDI	−1.17	1.03	1.15	n.s.
		N patches	−0.54	0.37	1.94	n.s.
		Amount of natural vegetation	−0.09	0.36	0.25	n.s.
		Distance from buildings	<0.01	<0.01	0.28	n.s.
		Distance from water	−0.01	0.01	1.11	n.s.
		Year	0.03	0.08	0.01	n.s.
		Month	0.01	0.01	0.16	n.s.
<i>Eptesicus serotinus</i>	0.28	<i>Intercept</i>	9.10	3.34	7.85	**
		Treatment	3.54	4.50	1.65	*
		Herd size	0.21	0.16	7.50	***
		Amount of edge habitat	0.01	0.14	1.92	n.s.
		SHDI	−0.41	1.89	0.06	n.s.
		N patches	0.13	0.67	1.31	n.s.
		Amount of natural vegetation	0.05	0.65	0.13	n.s.
		Distance from buildings	0.01	0.01	0.03	n.s.
		Distance from water	−0.01	0.01	0.15	n.s.
		Year	0.02	0.03	0.11	n.s.
		Month	0.02	0.11	0.11	n.s.
<i>Rhinolophus ferrumequinum</i>	0.46	<i>Intercept</i>	4.56	1.76	8.43	**
		Treatment	1.32	0.90	2.56	*
		Herd size	−0.06	0.03	2.58	n.s.
		Amount of edge habitat	<0.01	<0.01	0.08	n.s.

Table 2 (Continued)

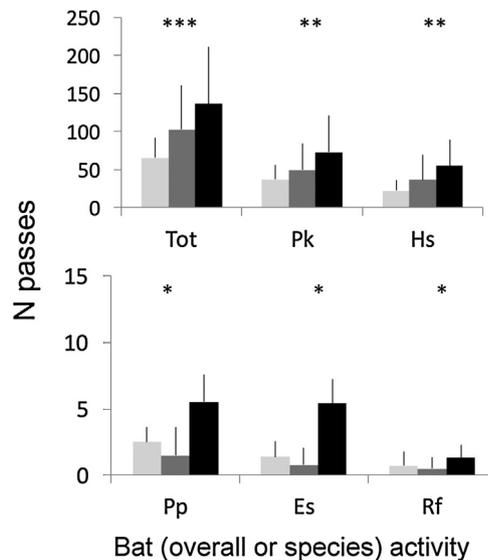
GLMM response	R <sup>2</sup>	Variable	Estimate	Error	Z	P
		SHDI	0.98	0.41	8.70	**
		N patches	-0.16	0.15	0.22	n.s.
		Amount of natural vegetation	0.03	0.14	0.01	n.s.
		Distance from buildings	<-0.01	<0.01	0.57	n.s.
		Distance from water	<0.01	<0.01	1.41	n.s.
		Year	0.01	0.01	0.36	n.s.
		Month	0.06	0.09	0.32	n.s.

SHDI=Shannon diversity index.

\* p < 0.05.

\*\* p < 0.01.

\*\*\* p < 0.001.



**Fig. 1.** Effect of treatment on bat activity. Numbers (mean  $\pm$  SD) of bat passes per point/recording night in an agro-pastoral area of central Italy. Black = cattle present; dark grey = dung only; light grey = control (pasture); significance of the 'treatment' effect: \*\*\*P < 0.001; \*\*P < 0.01; \*P < 0.05. Tot = Total bat activity; Pk = *Pipistrellus kuhlii*; Hs = *Hypsugo savii*; Pp = *Pipistrellus pipistrellus*; Es = *Eptesicus serotinus*; Rf = *Rhinolophus ferrumequinum*.

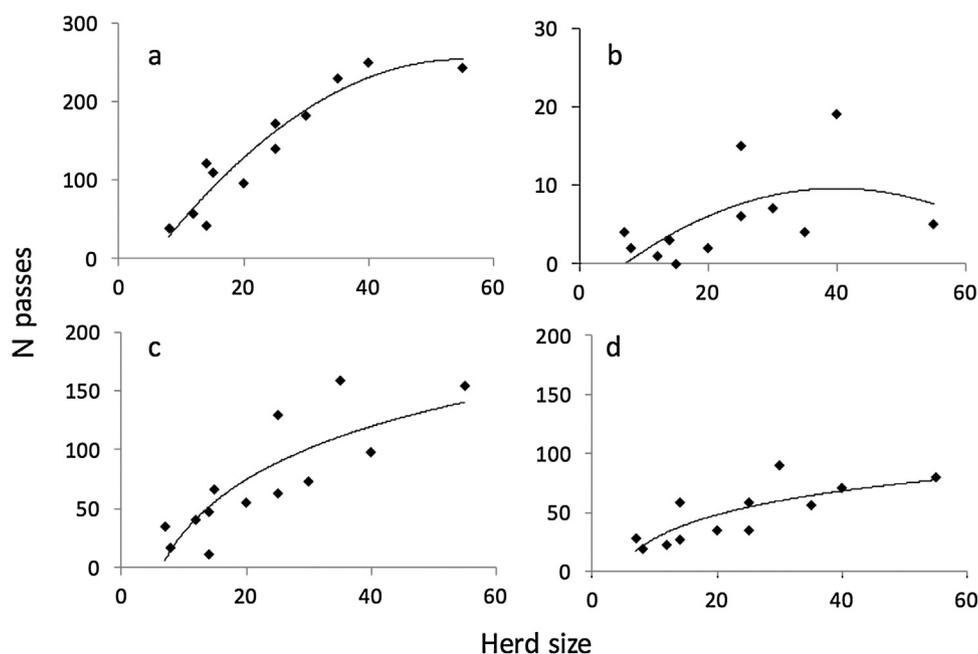
blood-sucking flies is substantial (Steelman, 1976; Byford et al., 1992), and the potential ecosystem service provided by bats in reducing these pests potentially very important (Reiskind and Wund, 2009). However, this relationship has yet to be studied in detail. Insects are stirred up by moving cattle during the day and a similar stirring up behaviour may also occur at night (Svensson et al., 2003), albeit this phenomenon is yet to be actually verified in the case of grazing cows. Although we cannot rule out that some prey was made available to bats in this way, it appears much more likely that the greatest portion of insects on which bats fed was represented by cattle's parasites, as livestock is known to attract large numbers of blood-sucking insects (e.g. Ceratopogonidae: Hayes et al., 1984; Culicidae: Petrarca et al., 1991; Service, 1993).

The bats that we recorded over cows belonged mostly to small, aerial-hawking species, i.e. those that typically feed on flying insects in the open air, such as pipistrelles (*Pipistrellus* spp., *Hypsugo savii*). However, these bats usually are most active within a few meters from trees and other vegetation, i.e. in "edge habitats" (Verboom and Huitema, 1997), which probably explains the observed positive effect of habitat heterogeneity on bat activity. Thus, it also seems likely that the bats did not feed exclusively on insects near the cows, but also those that occurred near vegetation. In our sample there were also observations of bats of the genus *Myotis*; this includes species that feed on insects on or very close to

surfaces, and some *Myotis* species even roost in stables and feed on parasitic flies such as the blood-sucking stable fly *Stomoxys calcitrans* (Steck and Brinkmann, 2006). However, observations of such bats were surprisingly few in our case, but we have seen them foraging over cattle in other pastures in central Italy (D. Russo and J. Rydell, unpublished observations). We cannot completely rule out that some *Myotis* sp. were actually present above livestock but went undetected due to the relatively faint echolocation calls some species broadcast (Waters and Jones, 1995).

The numerous feeding buzzes emitted by bats foraging over livestock may constitute a powerful clue of foraging site quality as both conspecifics and heterospecifics sharing feeding habits might eavesdrop on them (Barclay, 1982; Gillam, 2007; Dorado-Correa et al., 2013). Bats such as pipistrelles are opportunistic and flexible predators exploiting a broad prey spectrum (Goiti et al., 2003) including tiny midges (Barlow, 1997) and may be expected to feed on insects swarming near livestock as soon as these become available in profitable numbers (Bell, 1980). Noticeably, *Rhinolophus ferrumequinum* also took advantage of livestock presence yet its activity did not increase for larger herds, perhaps due to the small numbers of bats present in the area. Rhinolophids are also difficult to detect given their high-frequency, strongly directional calls, so their activity may be underestimated in acoustic surveys (e.g. Russo and Jones, 2002). It is known that this bat may exploit dung-dwelling beetles, a seasonally abundant food resource (Jones, 1990). For this reason, UK farmers are subsidised to keep livestock near maternity roosts and improve conditions for reproductive females (Ransome and Hutson, 2000). Our study remarks the importance of encouraging the presence of cattle in the surroundings of important roosts besides protecting existing roosts or providing further roosting opportunities when needed.

We found that bat foraging activity was higher at larger herds but eventually reached a plateau or even showed a slight decline. Assuming herd size as a proxy for prey density, this represents a typical type-II predator functional response (Holling, 1959): after a first boost in which predation rate successfully tracks increases in prey density being only limited by searching efficiency, a deceleration is observed and an asymptotic value reached over certain thresholds of prey abundance, essentially due to constraints posed by handling time. Type II functional responses are common among vertebrates (e.g. Poole et al., 2007; Smith and Smith, 2015). This suggests that insect suppression may increase for larger herds yet it might not keep the pace with exceedingly large ones. Bats are also unlikely to tolerate competition beyond a certain density and the spacing out of foraging bats typically occurs through agonistic behaviour such as chases and/or social calls (Rydell, 1986; Barlow and Jones, 1997). Alternatively, the drop in the increase of bat activity may be a genuine effect of lower insect abundances around herds, as aggregating represents a defensive strategy by herbivores to decrease blood-sucking insect density (Schmidtman and Valla, 1982). In a long term, the presence of large livestock herds might also decrease habitat complexity by



**Fig. 2.** Effect of herd size on bat activity. Polynomial regressions between numbers of bat passes and cattle herd size; (a) total bat activity ( $R^2 = 0.90$ ,  $p < 0.01$ ), (b) *Pipistrellus pipistrellus* ( $R^2 = 0.35$ ,  $p < 0.05$ ), (c) *Pipistrellus kuhlii* ( $R^2 = 0.68$ ,  $p < 0.05$ ), (d) *Hypsugo savii* ( $R^2 = 0.62$ ,  $p < 0.05$ ).

overgrazing and trampling, which inhibit the growth of woody vegetation, outweighing the positive effect of herd size on bat foraging and, in turn, insect suppression by bats. Our results in fact emphasise the role of “landscape” diversity in pastoral landscapes, in agreement with several other studies that show its role in supporting more diverse bat communities (Medina et al., 2007; Avila-Cabadilla et al., 2012). In our case this factor was the only one that influenced positively species richness besides bringing about positive effects on bat activity.

Bat foraging over livestock is almost certainly a hard-wired behaviour that evolved long before pastoralism, i.e. in association with herds of Pleistocene megaherbivores that created and maintained extensive grasslands (Hearn, 2015), and might be also associated with modern herds of wild ungulates such as deer and wild boars. Overall, our work highlights the value of traditional pastoralism for bat conservation, as livestock provide food to bats both directly and indirectly, through commensal and parasitic insects (this study), but also because moderate grazing contributes to more diverse landscapes in many ways (Fuhlendorf et al., 2006). Pastoral abandonment may thus threaten bats more than expected, so we strongly advocate for reintroduction of livestock at moderate densities in abandoned rangeland whenever feasible, not only in the Mediterranean region, but possibly throughout Europe.

A limitation of our study is that we could not assess the presence of livestock ectoparasites in bat diet, which would have required capturing bats foraging over livestock to collect fresh droppings. However, we remark that a considerable presence of insects potentially harmful to livestock among bat prey is highly probable, so that bats were more likely to act as mutualists than commensals. Culicids represent staple food for small-sized bats (Gonsalves et al., 2013) such as *P. kuhlii* (Goiti et al., 2003), the species that we recorded most frequently over livestock. Culicids are very harmful to free-ranging livestock by affecting their weight and milk production and by transmitting many zoonotic diseases, often resulting in the loss of many head (Steelman, 1976; Byford et al., 1992). The presence of bats on farm might thus be encouraged to represent a potentially important, so far neglected, way to help counter such effects. In geographical regions

affected by malaria, livestock attract the *Anopheles* mosquito vector, reducing insect bites on humans (Futami et al., 2014). Whether bats might suppress malaria-carrying mosquitoes over livestock strengthening this control action by reducing the number of insects also merits investigation, as small aerial-hawking bats feeding on mosquitoes can perform very efficient capture rates for prolonged periods each night (10 capture attempts/min for several hours, with success rate close to 100%: Rydell et al., 2002). Our results highlight the urgency to further investigate the reciprocal importance of traditional agropastoralism, which maintains habitat diversity and provides fundamental habitat elements such as food resources, and wildlife, which in the case of bats provide important ecosystem services such as pest control.

#### Acknowledgements

We are grateful to Alessia De Lorenzis for her fundamental support during all fieldwork activities, to the Azienda Agricola “Castel di Guido” and Roma Capitale for providing accommodation and access to the study area. Thanks also go to two anonymous reviewers whose comments helped us to improve substantially a first ms version. LA was funded by Lega Italiana Protezione Uccelli (LIPU onlus). IB was funded by the Erasmus+ Programme within the framework of an agreement between University of Naples Federico II and University of Belgrade.

#### References

- Alkemade, R., Reid, R.S., van den Berg, M., de Leeuw, J., Jeuken, M., 2013. Assessing the impacts of livestock production on biodiversity in rangeland ecosystems. *PNAS* 110, 20900–20905.
- Avila-Cabadilla, L.D., Sanchez-Azofeifa, G.A., Stoner, K.E., Alvarez-Añorve, M.Y., Quesada, M., Portillo-Quintero, C.A., 2012. Local and landscape factors determining occurrence of phyllostomid bats in tropical secondary forests. *PLoS One* 7 (4), e35228.
- Barclay, R.M.R., 1982. Interindividual use of echolocation calls – eavesdropping by bats. *Behav. Ecol. Sociobiol.* 10, 271–275.
- Barlow, K.E., Jones, G., 1997. Function of pipistrelle social calls: field data and a playback experiment. *Anim. Behav.* 53 (5), 991–999.
- Barlow, K., 1997. The diets of two phonic types of the bat *Pipistrellus pipistrellus* in Britain. *J. Zool. Lond.* 243, 597–609.

- Bell, G.P., 1980. Habitat use and response to patches of prey by desert insectivorous bats. *Can. J. Zool.* 58, 1876–1883.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18, 182–188.
- Blondel, J., Aronson, J., 1999. *Biology and Wildlife of the Mediterranean Region*. Oxford University Press, USA.
- Boitani, L., 2000. Carnivore introductions and invasions: their success and management. In: Funk, S., Gittleman, J., Macdonald, D.W., Wayne, R. (Eds.), *Carnivore Conservation*. Cambridge University Press, Cambridge, pp. 123–144.
- Boughey, K.L., Lake, I.R., Haysom, K.A., Dolman, P.M., 2011. Improving the biodiversity benefits of hedgerows: how physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. *Biol. Conserv.* 144, 1790–1798.
- Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.H., 2011. Economic importance of bats in agriculture. *Science* 332 (6025), 41–42.
- Byford, R.L., Craig, M.E., Crosby, B.L., 1992. A review of ectoparasites and their effect on cattle production. *J. Anim. Sci.* 70, 597–602.
- Caro, T., Darwin, J., Forrester, T., Ledoux-Bloom, C., Wells, C., 2012. Conservation in the anthropocene. *Conserv. Biol.* 26, 185–188.
- Catto, C.M.C., Hutson, A.M., Racey, P.A., Stephenson, P.J., 1996. Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *J. Zool.* 238, 623–633.
- Davies, L., 1957. A Study of the blackfly, *Simulium ornatum* Mg. (Diptera), with particular reference to its activity on grazing cattle. *Bull. Entomol. Res.* 48, 407–424.
- Donazar, J.A., Palacios, C.J., Gangoso, L., Ceballos, O., González, M.J., Hiraldo, F., 2002. Conservation status and limiting factors in the endangered population of Egyptian vulture (*Neophron percnopterus*) in the Canary Islands. *Biol. Conserv.* 107, 89–97.
- Dorado-Correa, A.M., Goerlitz, H.R., Siemers, B.M., 2013. Interspecific acoustic recognition in two European bat communities. *Front. Physiol.* 4.
- Downs, N.C., Racey, P.A., 2006. The use by bats of habitat features in mixed farmland in Scotland. *Acta Chiropterol.* 8, 169–185.
- Downs, N.C., Sanderson, L.J., 2010. Do bats forage over cattle dung or over cattle? *Acta Chiropterol.* 12, 349–358.
- Duvergé, P.L., Jones, G., 2003. Use of farmland habitats by greater horseshoe bats. In: Tattersall, F., Manley, W. (Eds.), *Conservation and Conflict: Mammals and Farming in Britain*. Linnean Society Occasional Publications 4. Westbury Publishing, Otley, UK, pp. 64–81.
- Federico, P., Hallam, T.G., McCracken, G.F., Purucker, S.T., Grant, W.E., Correa-Sandoval, A.N., Westbrook, J.K., Medellín, R.A., Cleveland, C.J., Sansone, C.G., López, J.D., Betke, M., Moreno-Valdez, A., Kunz, T.H., 2008. Brazilian free-tailed bat as insect pest regulators in transgenic and conventional cotton crops. *Ecol. Appl.* 18, 826–837.
- Fleischner, T.L., 1994. Ecological costs of livestock grazing in Western North America. *Conserv. Biol.* 8, 629–644.
- Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A., Leslie, D.M., 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecol. Appl.* 16, 1706–1716.
- Futami, K., Dida, G.O., Sonye, G.O., Lutiali, P.A., Mwanja, M.S., Wagalla, S., Lumumba, J., Kongere, J.O., Njenga, S.M., Minakawa, N., 2014. Impacts of insecticide treated bed nets on *Anopheles gambiae* s.l. populations in Mbita district and Suba district, Western Kenya. *Parasites Vectors* 7, 1.
- Gillam, E.H., 2007. Eavesdropping by bats on the feeding buzzes of conspecifics. *Can. J. Zool.* 85, 795–801.
- Goiti, U., Vecin, P., Garin, I., Saloña, M., Aihartza, J.R., 2003. Diet and prey selection in Kuhl's pipistrelle *Pipistrellus kuhlii* (Chiroptera: Vespertilionidae) in south-western Europe. *Acta Theriol.* 48, 457–468.
- Gonsalves, L., Bicknell, B., Law, B., Webbm, C., Monamym, V., 2013. Mosquito consumption by insectivorous bats: does size matter? *PLoS One* 8 (10), e77183. doi:<http://dx.doi.org/10.1371/journal.pone.0077183>.
- Griffin, D.R., Webster, F.A., Michael, C.R., 1960. The echolocation of flying insects by bats. *Anim. Behav.* 8, 141–154.
- Hayes, M.E., Mullen, G.R., Nusbaum, K.E., 1984. Comparison of *Culicoides* spp. (Diptera: Ceratopogonidae) attracted to cattle in an open pasture and bordering woodland. *Mosq. News* 44, 368–370.
- Hearn, R., 2015. Gains and losses in the European mammals. In: Kiby, K.J., Watkins, C. (Eds.), *Europe's Changing Woods and Forests. From Wildwood to Managed Landscapes*. CABI, UK, USA, pp. 193–206.
- Heatwole, H., 1965. Some aspects of the association of Cattle Egrets with cattle. *Anim. Behav.* 13, 79–83.
- Heim, O., Treitler, J.T., Tschapka, M., Knörnschild, M., Jung, K., 2015. The importance of landscape elements for bat activity and species richness in agricultural areas. *PLoS One* 10 (7), e0134443.
- Heim, O., Schröder, A., Eccard, J., Jung, K., Voigt, C.C., 2016. Seasonal activity patterns of European bats above intensively used farmland. *Agric. Ecosyst. Environ.* 233, 130–139.
- Holling, C.S., 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* 91, 293–320.
- Hooke, R.L., Martín-Duque, J.F., Pedraza, J., 2012. Land transformation by humans: a review. *GSA Today* 22, 4–10.
- Jefferies, D.J., 1972. Organochlorine insecticide residues in British bats and their significance. *J. Zool. Lond.* 166, 245–263.
- Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R., Racey, P.A., 2009. Carpe noctem: the importance of bats as bioindicators. *Endanger. Species Res.* 8, 93–115.
- Jones, G., 1990. Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? *J. Anim. Ecol.* 59, 587–602.
- Kalcounis, M.C., Hobson, K.A., Brigham, R.M., Hecker, K.R., 1999. Bat activity in the boreal forest: importance of stand type and vertical strata. *J. Mamm.* 80, 673–682.
- Kazek, M., Jezierski, T., 2014. Ecological, behavioural and economic effects of insects on grazing farm animals—a review. *Anim. Sci. Pap. Rep.* 32, 107–119.
- Korine, C., Adams, A.M., Shamir, U., Gross, A., 2015. Effect of water quality on species richness and activity of desert-dwelling bats. *Mammal. Biol.* 80, 185–190.
- Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. *Ann. N. Y. Acad. Sci.* 1223, 1–38.
- López-González, C., Presley, S.J., Lozano, A., Stevens, R.D., Higgins, C.L., 2015. Ecological biogeography of Mexican bats: the relative contributions of habitat heterogeneity, beta diversity, and environmental gradients to species richness and composition patterns. *Ecography* 38, 261–272.
- Lumaret, J.P., Kirk, A., 1987. Ecology of dung beetles in the French Mediterranean region (Coleoptera: Scarabaeinae). *Acta Zool. Mex.* 24, 1–55.
- Maine, J.J., Boyles, J.G., 2015. Bats initiate vital agroecological interactions in corn. *Proc. Natl. Acad. Sci. U. S. A.* 112, 12438–12443.
- Marques, J.T., Rainho, A., Carapuço, M., Oliveira, P., Palmeirim, J.M., 2004. Foraging behaviour and habitat use by the European free-tailed bat *Tadarida teniotis*. *Acta Chiropterol.* 6, 99–110.
- McCracken, G.F., Westbrook, J.K., Brown, V.A., Eldridge, M., Federico, P., Kunz, T.H., 2012. Bats track and exploit changes in insect pest populations. *PLoS One* 7 (8), e43839.
- McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst Available at the following web site: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- Medina, A., Harvey, C.A., Merlo, D.S., Vilchez, S., Hernández, B., 2007. Bat diversity and movement in an agricultural landscape in Matiguás, Nicaragua. *Biotropica* 39 (1), 120–128.
- Moreira, F., Russo, D., 2007. Modelling the impact of agricultural abandonment and wildfires on vertebrate diversity in Mediterranean Europe. *Landscape Ecol.* 22, 1461–1476.
- Moreira, F., Pinto, M.J., Henriques, I., Marques, T., 2005. Importance of low-intensity farming systems for fauna, flora and habitats protected under the European "Birds" and "Habitats" directives: is agriculture essential for preserving biodiversity in the Mediterranean region? In: Burk, A.R. (Ed.), *Trends in Biodiversity Research*. Nova Science Publishers, New York, pp. 117–145.
- Morelli, F., Benedetti, Y., Ibáñez-Álamo, J.D., Jokimäki, J., Mänd, R., Tryjanowski, P., Møller, A.P., 2016. Evidence of evolutionary homogenization of bird communities in urban environments across Europe. *Global Ecol. Biogeogr.* 25, 1284–1293.
- Park, K.J., 2015. Mitigating the impacts of agriculture on biodiversity: bats and their potential role as bioindicators. *Mammal. Biol.* 80, 191–204.
- Parker, T.S., Nilon, C.H., 2012. Urban landscape characteristics correlated with the synurbanization of wildlife. *Landscape Urban Plan.* 106, 316–325.
- Petrarca, V., Beier, J.C., Onyango, F., Koros, J., Asiago, C., Koech, D.K., Roberts, C.R., 1991. Species composition of the *Anopheles gambiae* complex (Diptera: Culicidae) at two sites in western Kenya. *J. Med. Entomol.* 28, 307–313.
- Petretti, F., 2003. *Gestione della Fauna*. Edagricole, Bologna, Italy.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., Maintainer, R., 2016. Package 'nlme'.
- Poole, A.E., Stillman, R.A., Watson, H.K., Norris, K.J., 2007. Searching efficiency and the functional response of a pause-travel forager. *Funct. Ecol.* 21, 784–792.
- Puig-Montserrat, X., Torre, I., López-Baucells, A., Guerrieri, E., Monti, M.M., Ràfols-García, R., Ferrer, X., Gisbert, D., Flaquer, C., 2015. Pest control service provided by bats in Mediterranean rice paddies: linking agroecosystems structure to ecological functions. *Mamm. Biol.* 80, 237–245.
- R Development Core Team, 2011. *R: A language and environment for statistical computing*. Vienna, Austria : the R Foundation for Statistical Computing ISBN: 3-900051-07-0. Available online at <http://www.R-project.org/>.
- Ransome, R.D., Hutson, A.M., 2000. Action Plan for the conservation of the greater horseshoe bat in Europe (*Rhinolophus ferrumequinum*). Convention on the Conservation of European Wildlife and Natural Habitats, Nature and Environment 109. Council of Europe Publishing.
- Ransome, R.D., 1996. The management of feeding areas for greater horseshoe bats English Nature Research Reports. Peterborough 174, 1–74.
- Reiskind, M.H., Wund, M.A., 2009. Experimental assessment of the impacts of northern long-eared bats on ovipositing *Culex* (Diptera: Culicidae) mosquitoes. *J. Med. Entomol.* 46, 1037–1044.
- Russo, D., Jones, G., 2002. Identification of twenty-two bat species (Mammalia: Chiroptera) from Italy by analysis of time-expanded recordings of echolocation calls. *J. Zool.* 258, 91–103.
- Russo, D., Jones, G., 2003. Use of foraging habitats by bats (Mammalia: Chiroptera) in a Mediterranean area determined by acoustic surveys: conservation implications. *Ecography* 26, 197–209.
- Russo, D., Jones, G., 2015. Bats as bioindicators: an introduction. *Mammal. Biol.* 80, 157–158.
- Russo, D., Voigt, C.C., 2016. The use of automated identification of bat echolocation calls in acoustic monitoring: a cautionary note for a sound analysis. *Ecol. Indic.* 66, 598–602.

- Russo, D., Jones, G., Migliozi, A., 2002. Habitat selection by the Mediterranean horseshoe bat, *Rhinolophus euryale* (Chiroptera: Rhinolophidae) in a rural area of southern Italy and implications for conservation. *Biol. Conserv.* 107, 71–81.
- Russo, D., Almenar, D., Aihartza, J., Goiti, U., Salsamendi, E., Garin, I., 2005. Habitat selection in sympatric *Rhinolophus mehelyi* and *R. euryale* (Mammalia: Chiroptera). *J. Zool.* 266, 327–332.
- Russo, D., Ancillotto, L., Cistrone, L., Korine, C., 2016. The buzz of drinking on the wing in echolocating bats. *Ethology* 122, 226–235.
- Rydell, J., Parker McNeill, D.P., Eklöf, J., 2002. Capture success of little brown bats (*Myotis lucifugus*) feeding on mosquitoes. *J. Zool. Lond.* 256, 379–381.
- Rydell, J., 1986. Feeding territoriality in female northern bats. *Eptesicus nilssoni*. *Ethology* 72, 329–337.
- Schmidtman, E.T., Valla, M.E., 1982. Face-fly pest intensity, fly-avoidance behavior (bunching) and grazing time in Holstein heifers. *Appl. Anim. Ethol.* 8, 429–438.
- Service, M.W., 1993. Sampling adults by animal bait catches and by animal-baited traps. In: Service, M.W. (Ed.), *Mosquito Ecology: Field Sampling Methods*. Chapman & Hall, London, UK, pp. 349–498.
- Shiel, C.B., McAney, C.M., Fairley, J.S., 1991. Analysis of the diet of Natterer's bat *Myotis nattereri* and the common long-eared bat *Plecotus auritus* in the West of Ireland. *J. Zool.* 223, 299–305.
- Singh, J.S., 2002. The biodiversity crisis: a multifaceted review. *Curr. Sci.* 82, 638–647.
- Smith, T.M., Smith, R.L., 2015. *Elements of Ecology*, 9th edition Pearson.
- Smith, L.A., White, P.C., Marion, G., Hutchings, M.R., 2009. Livestock grazing behavior and inter-versus intraspecific disease risk via the fecal-oral route. *Behav. Ecol.* 20, 426–432.
- Stamper, T., DeBry, R.W., 2007. The nocturnal oviposition behavior of carrion flies in rural and urban environments: methodological problems and forensic implications. *Can. Soc. Forensic Sci. J.* 40, 173–182.
- Steck, C.E., Brinkmann, R., 2006. The trophic niche of the Geoffroy's bat (*Myotis emarginatus*) in south-western Germany. *Acta Chiropterol.* 8, 445–450.
- Stelman, C.D., 1976. Effects of external and internal arthropod parasites on domestic livestock production. *Annu. Rev. Entomol.* 21, 155–178.
- Svensson, A.M., Eklöf, J., Skals, N., Rydell, J., 2003. Light dependent shift in the anti-predator response of a pyralid moth. *Oikos* 101, 239–246.
- Turner, W.R., Brandon, K., Brooks, T.M., Costanza, R., Da Fonseca, G.A., Portela, R., 2007. Global conservation of biodiversity and ecosystem services. *BioScience* 57, 868–873.
- Vaughan, N., Jones, G., Harris, S., 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *J. Appl. Ecol.* 34, 716–730.
- Verboom, B., Huitema, H., 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecol.* 12, 117–125.
- Wahungu, G.M., Mumia, E.N., Manoa, D., 2003. The effects of flock size, habitat type and cattle herd sizes on feeding and vigilance in cattle egrets (*Ardeola ibis*). *Afr. J. Ecol.* 41, 287–288.
- Waters, D.A., Jones, G., 1995. Echolocation call structure and intensity in five species of insectivorous bats. *J. Exp. Biol.* 198, 475–489.
- Wickramasinghe, L.P., Harris, S., Jones, G., Vaughan, N., 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. *J. Appl. Ecol.* 40, 984–993.
- Wickramasinghe, L.P., Harris, S., Jones, G., Jennings, N.V., 2004. Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. *Conserv. Biol.* 18, 1283–1292.
- Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., Bradbury, R.B., 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agric. Ecosyst. Environ.* 75, 13–30.